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Implications of stunting on morphology of freshwater fishes

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The purpose of this study was to assess morphological differences between stunted and non-stunted white perch *Morone americana* and green sunfish *Lepomis cyanellus*. Few female *M. americana* were captured; thus, morphological differences between adult males and juveniles were assessed for *M. americana*. Similarly, few immature (juvenile) *L. cyanellus* were captured for the stunted morphotype; thus, male and female morphological differences were assessed for *L. cyanellus*. Features of the head tended to be relatively larger in stunted fish of both species, whereas the mid-body tended to be relatively larger in non-stunted *M. americana*, but not in non-stunted *L. cyanellus*. Adult and juvenile morphology overlapped considerably in non-stunted *M. americana*, but there was a clear distinction between adult and juvenile morphology of stunted *M. americana*. There was little sexual dimorphism in shape in stunted *L. cyanellus*, whereas sexual dimorphism was evident in non-stunted *L. cyanellus*. It appears that selective forces imposed by predation and food limitation may contribute to morphological diversification between stunted and non-stunted fishes.
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Key words: body shape; *Lepomis cyanellus*; *Morone americana*; morphometry; stunted fishes.

INTRODUCTION

Stunted populations are frequently observed in fishes (Roff, 1992). Chizinski (2007) defined a stunted population as consisting of individuals that grow slowly and mature early and at a small size, in which growth is restricted by density-dependent mechanisms, and the diminished maximum size is not genetically determined. Several ecological factors, including increased survival from reduced predation and decreased food availability, may influence the development of individuals in stunted populations (Roff, 1992; Ylikarjula *et al*., 1999; van Kooten *et al*., 2007). Predation is an important population structuring mechanism, which has a close relationship to prey density and, hence, density-dependent food limitation (Anders, 2001), and which imposes a strong selective pressure at the individual level (Taborsky *et al*., 2003). When there is sufficient size selective mortality, relatively low density-dependent food limitation,

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and the presence of a size refuge (determined by the interaction of predation risk and prey morphology), life-history theory predicts that fishes should delay reproduction and grow to a larger asymptotic size (Stearns, 1989, 1992; Roff, 1992; Taborsky, 2006). Alternatively, when predation risk is minimal, density-dependent food limitation is sufficiently strong and growth rate of fishes limited, life-history theory predicts early reproduction and a smaller asymptotic size (Stearns, 1989, 1992; Roff, 1992; Taborsky, 2006).

In addition to influencing population structure in fishes, predation has been observed to affect body morphology (Brönmark & Miner, 1992; Januszkiewicz & Robinson, 2007). Brönmark & Miner (1992) observed that in ponds containing gape-limited predators, *e.g.* pike *Esox lucius* L., there were low densities of large-sized crucian carp *Carassius carassius* (L.), whereas in ponds without predators there were high densities of small-sized *C. carassius*. In the presence of predators, *C. carassius* were relatively deeper bodied, an adaptive, environmentally induced response to minimize predation risk by gape-limited predators. Morphological responses to predation risk also were described in pumpkinseed *Lepomis gibbosus* (L.) in response to walleye *Sander vitreus* (Mitchell) predation (Januszkiewicz & Robinson, 2007) and in mosquitofish *Gambusia affinis* (Baird & Girard), which displayed a shape change that was consistent with faster burst-swim response (Langerhans *et al*., 2004).

The morphological effects of the interaction between predation and food limitation are less well known. In a series of experiments, Chivers *et al*. (2008) examined the effects of food availability and predation on the growth and morphology of goldfish *Carassius auratus* (L.). They observed that food level affected the magnitude of the morphological changes in response to predation. For example, *C. auratus* under low food availability and in the presence of predation displayed smaller changes in body depth than did *C. auratus* exposed to predation without food limitation. Stunted fishes, compared with their non-stunted conspecifics, would be good subjects to provide further analysis of this interaction. Given the role of predation and food limitation in influencing the development of a stunted population, it is expected that these influences would be manifested in the morphologies of individuals in stunted and non-stunted populations. In non-stunted fishes, it is expected that morphology is largely influenced by predation, whereas in stunted fishes it is expected that morphology is largely influenced by food limitation (Fig. 1). Thus, the purpose of this study was to assess morphological differences between stunted and non-stunted morphotypes of two freshwater fish species that have a propensity to stunt. In addition to assessing morphological differences between the two morphotypes,

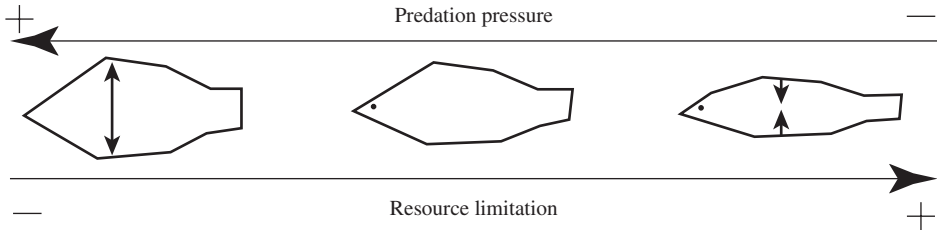

FIG. 1. Conceptualization of the factors associated with stunting and the morphological implications of those factors in fishes.

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differences between juvenile and adult forms and between male and female forms were assessed. Several predictions were made concerning morphological differentiation between stunted and non-stunted fishes: 1) there would be clear differentiation in body form between stunted and non-stunted fishes, 2) due to rapid growth rates in the non-stunted fishes, there would be greater differentiation between juvenile and adult forms than in stunted fishes and 3) energy limitations of stunted fishes would constrain the degree of differentiation among the male and female morphologies. Studying differences in morphological expression among the stunted and non-stunted morphotypes should provide insight into the interaction of predation and food limitation in fishes.

MATERIALS AND METHODS

STUDY SPECIES

Morphological assessments of stunted and non-stunted fishes focused on two species that frequently exhibit the stunted morphotype. White perch *Morone americana* (Gmelin) is a pelagic species native to the east coast of North America (Scott & Crossman, 1973). *Morone americana* have invaded many water bodies throughout the U.S.A. and has a propensity to form stunted populations (Hergenrader & Bliss, 1971; Hergenrader, 1980; Wong, 2002). Green sunfish *Lepomis cyanellus* Rafinesque is a littoral sunfish found throughout North America (Lever, 1996). *Lepomis cyanellus* also has a propensity to form stunted populations in water bodies lacking predators (Moyle, 2000). There have been no previous assessments of the morphology of *M. americana* or *L. cyanellus* in the primary literature. Chizinski (2007) analysed life-history and demographic variables between two populations of each species, which provided the justification for the stunted and non-stunted designations.

STUDY SITES

Branched Oak Lake (40° 58′ N; 96° 51′ W), a 728 ha flood-control reservoir in Lancaster County, Nebraska, was completed in 1967. This reservoir had a fish community consisting of bluegill *Lepomis macrochirus* Rafinesque, common carp *Cyprinus carpio* L., blue catfish *Ictalurus furcatus* (Valenciennes), channel catfish *Ictalurus punctatus* (Rafinesque), flathead catfish *Pylodictis olivaris* (Rafinesque), crappie *Pomoxis* spp., largemouth bass *Micropterus salmoides* (Lacépède), palmetto bass *Morone saxatilis* (Walbaum) × *Morone chrysops* (Rafinesque), *S. vitreus*, gizzard shad *Dorosoma cepedianum* (Lesueur) and *M. americana*. All species except *C. carpio* and *D. cepedianum* are potential predators of adult *M. americana*. Since their establishment in Branched Oak Lake (Vrtiska *et al*., 2003), *M. americana* steadily increased in abundance ultimately achieving a large, stable but stunted population.

Pawnee Lake (40° 50′ N; 96° 52′ W), a 299 ha flood-control reservoir in Lancaster County, Nebraska, was completed in 1964. This reservoir is located 14 km south of Branched Oak Lake. Pawnee Lake had a fish community consisting of *C. carpio*, *I. punctatus*, *P. olivaris*, *Pomoxis* spp., freshwater drum *Aplodinotus grunniens* Rafinesque, *M. salmoides*, *M. chrysops*, sauger *Sander canadensis* (Griffith & Smith), *S. vitreus* and *M. americana*. All species except *C. carpio* and *A. grunniens* are potential predators of adult *M. americana*. Since becoming established in Pawnee Lake, *M. americana* have not become overly abundant, and grow to a larger maximum size than *M. americana* in Branched Oak Lake (Fig. 2).

Justiceburg Pond (33° 00′ N; 101° 11′ W) was surrounded by native grasslands on the Texas Tech University Experimental Ranch near Justiceburg, Texas, and had a 0·25 ha surface area and a maximum depth of 3 m. Only *L. cyanellus* occurred in this pond. A high incidence of cannibalism in adult *L. cyanellus* was observed in Justiceburg Pond (C. J. Chizinski, unpubl. data). The maximum size of *L. cyanellus* in Justiceburg Pond (Fig. 2) was similar to typical lengths for this species (Moyle, 2000).

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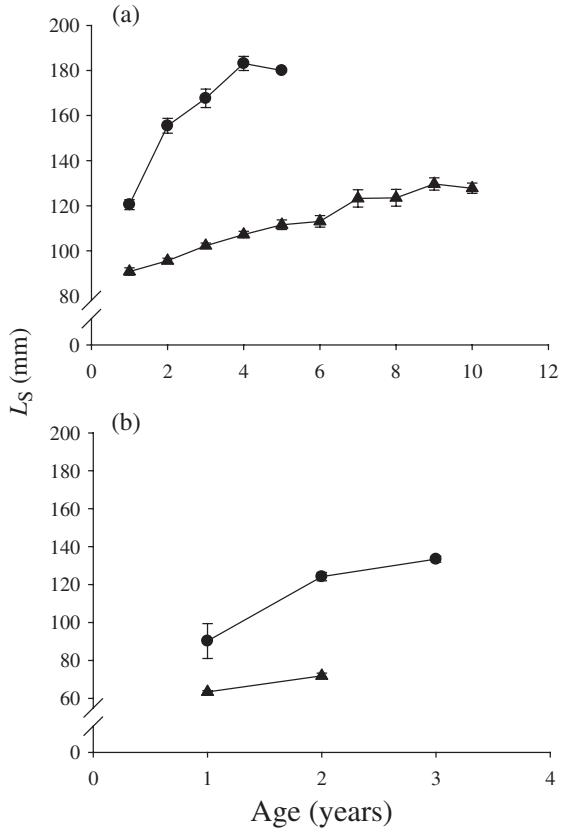

FIG. 2. Mean ± S.E. standard length (L_S) at age for stunted (▲) and non-stunted (●) (a) *Morone americana* and (b) *Lepomis cyanellus* sampled during 2006.

Mahon Pond (33° 33′ N; 101° 55′ W) was surrounded by an urban park in Lubbock, Texas, and had a 0·4 ha surface area and a maximum depth of 2 m. Mahon Pond is located 87 km north-west of Justiceburg Pond. The fish community of Mahon Pond consisted of black bullhead *Ameiurus melas* (Rafinesque), *C. carpio*, *C. auratus* and *L. cyanellus*. No evidence of cannibalism for *L. cyanellus* was observed in Mahon Pond (C. J. Chizinski, unpubl. data) and *A. melas* were the only potential predator. The Mahon Pond *L. cyanellus* exhibited decreased growth compared to *L. cyanellus* from Justiceburg Pond (Fig. 2).

FISH SAMPLING

Species-specific fish-collection protocols were used because of variation in habitat size and spawning behaviour. *Morone americana* primarily occupy limnetic habitats and spawn during a brief (2–3 weeks) period, whereas *L. cyanellus* occupy littoral habitats and spawn during a protracted (20–24 weeks) period. *Morone americana* were collected during April 2006 prior to the onset of spawning, with a Smith-Root 5.0 GPP boat electrofisher (pulsed DC) (www.smith-root.com) from Branched Oak Lake and Pawnee Lake. *Lepomis cyanellus* were collected at biweekly intervals from March until November 2006 with a Smith-Root backpack shocker and a Smith-Root 5.0 GPP boat electrofisher (pulsed DC) from Justiceberg Pond and Mahon Pond. A lethal dose (1 g l^{-1}) of MS-222 was used to euthanize all fishes. Later, fishes were stored on ice until processed in the laboratory.

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MORPHOLOGICAL ANALYSES

Digital photographs of unpreserved individual fishes were taken in the laboratory and digitized using tpsDig (Rohlf, 2006). Thirteen landmarks corresponding to 25 measurements coincided with major points on the outline of the body and the location of the pectoral fin and midpoint of the eye for *M. americana* and *L. cyanellus* (Fig. 3). A set of 25 pair-wise distances among landmarks in the form of a truss (Strauss & Bookstein, 1982) were used for subsequent morphological analyses. Each fish was categorized based on morphotype and reproductive status (*i.e.* stunted juvenile, stunted adult, non-stunted juvenile and non-stunted adult) for *M. americana* and gender (*i.e.* stunted male, stunted female, non-stunted male and non-stunted female) for *L. cyanellus*. Gender and reproductive status were determined by macro-inspection of the gonads. Few female *M. americana* were captured ($n = 16$ for Branched Oak Lake; $n = 1$ for Pawnee Lake); thus, female *M. americana* were omitted from analysis to prevent potential biases caused by sexual dimorphism. Similarly, few immature (juvenile) *L. cyanellus* were captured for the stunted morphotype ($n = 8$ for Mahon Pond); thus, immature *L. cyanellus* were omitted from analysis to prevent potential biases caused by sexual maturity.

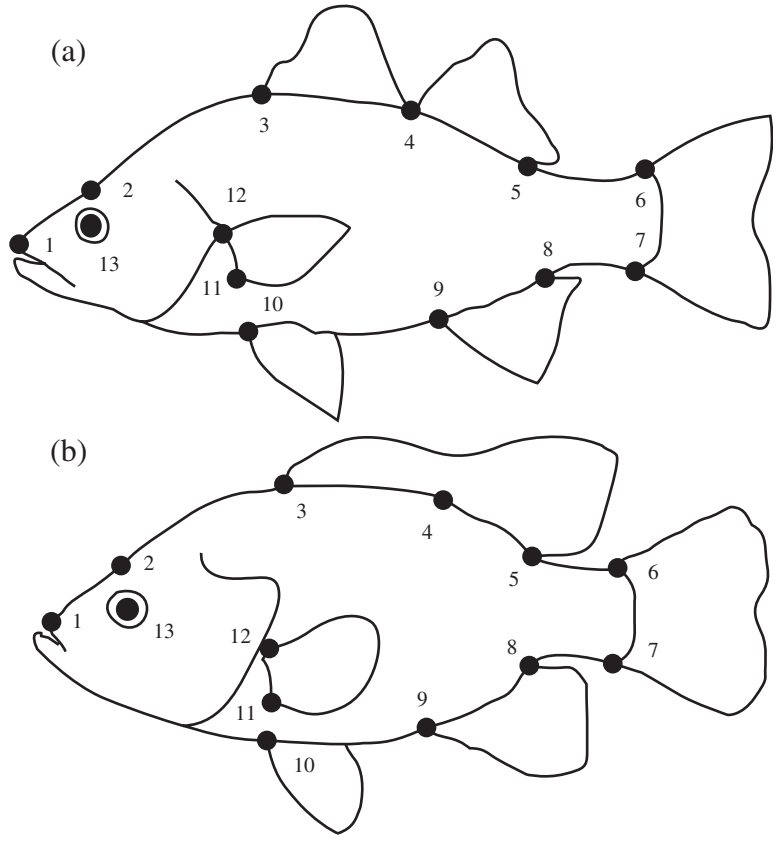

FIG. 3. Landmarks used in the morphological analysis of a (a) *Morone americana* and (b) *Lepomis cyanellus*: 1, snout tip; 2, inflection point on head; 3, origin of dorsal-fin base; 4, split in dorsal-fin base or origin of soft-ray base; 5, end of dorsal-fin base; 6, dorsal origin of caudal-fin base; 7, ventral origin of caudal-fin base; 8, end of anal-fin base; 9, origin of anal-fin base; 10, origin of pelvic-fin base; 11, end of pectoral-fin base; 12, origin of pectoral-fin base; 13, centre of the eye.

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A combination of traditional and geometric morphometric analyses was used to assess differences among *a priori* group designations. Discriminant function analysis (DFA) on ln-transformed interlandmark distances between co-ordinates was used to assess differences between groups. The size of *M. americana* in Branched Oak Lake and *L. cyanellus* in Mahon Pond was, by nature, smaller than that of *M. americana* in Pawnee Lake and *L. cyanellus* in Justiceburg Pond, thus requiring correction for size differences. A size-free DFA (Dos Reis *et al*., 1990) was used. Briefly, this method calculates size-free canonical variables by 1) finding the pooled within-group principal components, 2) regressing characters independently on the first within-group principal component, which characterized size variation from each truss character independently, 3) restoring the group centroids and 4) using the regression residuals in a canonical discriminant analysis. More detail of this process is provided by Strauss (1995). Multivariate analysis of variance (MANOVA) between morphotype, reproductive status or sex, and the associated interaction was used to assess the morphological divergence between groups. Statistical significance of the distance was assessed at $\alpha = 0{\cdot}05$. Jackknifed size-free, ln-transformed morphological characters were used to estimate misclassification error rates. In addition to determining whether shape differences were evident between *a priori* groupings, loadings (correlations between the size-free distances and the discriminant function scores) identified distinguishing morphological characteristics. It was assumed that variables with an absolute loading $>0{\cdot}30$ contributed significantly to shape variation. DFA and classification error analysis utilized a Matlab toolbox (www.matlab.com) (Strauss, 2007) in Matlab (v. 6.5).

Consensus plots were used to construct deformation grid plots in tpsSplin (Rohlf, 1994). Deformation grids describe the warping necessary to transform one form into another. If two morphotypes are identical, the output grid will contain straight lines where intersections of all elements are 90° angles. Deformation between non-stunted juvenile and stunted juvenile, non-stunted adult and stunted adult, stunted juvenile and stunted adult, and non-stunted juvenile and non-stunted adult morphotypes for *M. americana*; and between non-stunted male and stunted male, non-stunted female and stunted female, stunted male and stunted female, and non-stunted male and non-stunted female morphotypes for *L. cyanellus* was assessed. Among comparisons between stunted and non-stunted morphotypes, the non-stunted consensus plot was the reference form. Among comparisons between juvenile and adult forms, the juvenile consensus plot was the reference form. Among comparisons between male and female forms, the male consensus plot was the reference form.

RESULTS

FISH SAMPLING

A total of 226 *M. americana* and 248 *L. cyanellus* was collected for morphological analysis. Among the *M. americana*, there were 31 stunted juveniles, 60 stunted adults, 22 non-stunted juveniles and 113 non-stunted adults. Among *L. cyanellus*, there were 59 stunted males, 58 stunted females, 83 non-stunted males and 48 non-stunted females.

MORONE AMERICANA

Growth comparisons

Bivariate plots of canonical loadings of morphological distances from the DFA revealed distinct differences in morphology between stunted and non-stunted *M. americana*. Based on visual inspection of the DFA plot, the separation between stunted and non-stunted morphotypes occurred along the first discriminant axis (Fig. 4), which explained 88·7% of the variation in morphological distances. Discrimination on this axis was contributed to by 21 measurements, with differences

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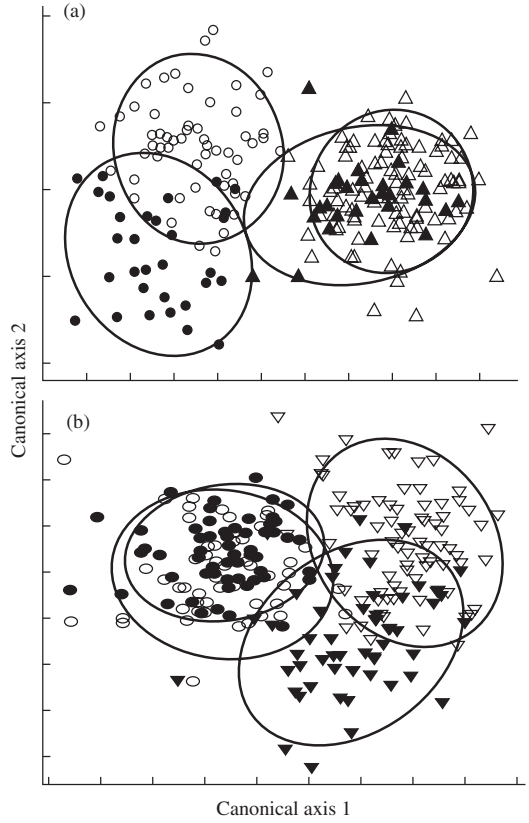

FIG. 4. (a) Canonical roots from discriminant function analysis of *Morone americana* classified by morphotype and reproductive status: stunted juvenile (●), stunted adult (○), non-stunted juvenile (▲) and non-stunted adult (△). (b) Canonical roots from discriminant function analysis of *Lepomis cyanellus* classified by morphotype and gender: stunted male (⬭), stunted female (●), non-stunted male (▽) and non-stunted female (▼). Ellipses represent the 95% CI around the canonical-root centroid for each group.

among the two morphotypes concentrated within three distinct zones: head, preanal body and postanal body. Morphological differences attributable to features in the head and postanal region tended to be greater for stunted *M. americana* than for non-stunted *M. americana*, whereas differences attributable to preanal body tended to be greater for non-stunted *M. americana* (Fig. 5). The morphological separation among stunted and non-stunted *M. americana* was predominantly attributable to four characteristics: the tip of the snout to the centre of the eye, centre of the eye to the origin of the pectoral-fin base, the split in the dorsal fin to the origin of the anal-fin base and the end of the dorsal-fin base to the end of the anal-fin base (Fig. 5).

There were significant differences (MANOVA, d.f. $= 25, 198$, $P < 0{\cdot}001$) between stunted and non-stunted *M. americana* (Table I). Stunted juvenile *M. americana* and non-stunted adult *M. americana* demonstrated the greatest morphological separation. Few ($n = 4$ of 226) fish were incorrectly reclassified as stunted or non-stunted (Table II). The successful reclassification emphasized the clear morphological discrimination between stunted and non-stunted individuals.

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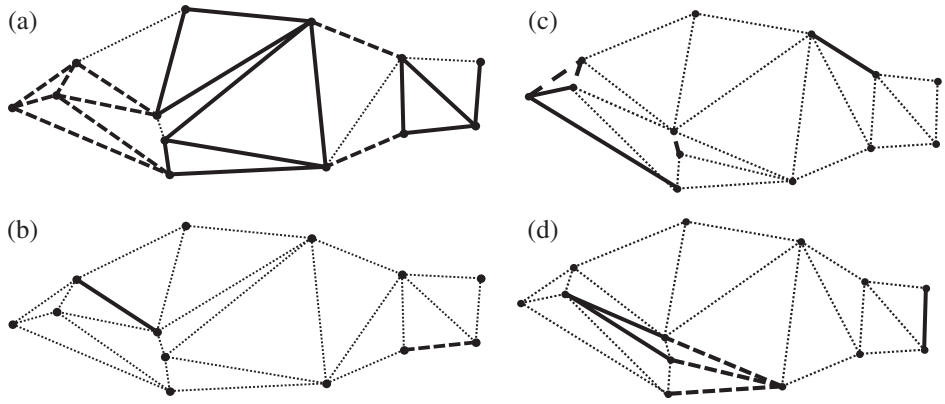

FIG. 5. Significant loadings and landmark co-ordinates between (a) stunted and non-stunted (first discriminant axis) and (b) adult and juvenile (second discriminant axis) *Morone americana* and co-ordinates between (c) stunted and non-stunted (first discriminant axis) and (d) male and female (second discriminant axis) *Lepomis cyanellus*. ___, morphological distances associated with positive loading values; - - -, morphological distances associated with negative loading values.

Ontogenetic comparisons

The ability to distinguish between juvenile and adult *M. americana* depended on morphotype and occurred along the second discriminant axis (based on visual inspection of the DFA plot), which explained 8·9% of the variation (Fig. 4). Juvenile and adult morphologies overlapped considerably for non-stunted *M. americana*, whereas stunted juvenile and adult *M. americana* morphologies showed clearer discrimination. The morphological separation among stunted *M. americana* was predominantly attributable to two characteristics: the distance from the end of the anal-fin base to the ventral origin of the caudal fin was greater in juvenile *M. americana*, whereas the distance from inflection point on the head to the origin of the pectoral fin was greater in adult *M. americana* (Fig. 5).

There were significant differences (MANOVA, d.f. = 25, 198; $P < 0{\cdot}001$) between the juvenile and adult *M. americana* (Table I). The associated interaction

TABLE I. Multivariate analysis of variance of ln-transformed distances for *Morone americana* and *Lepomis cyanellus*. Population is stunted or non-stunted and maturation is juvenile or adult

Factor	d.f. (N)	d.f. (D)	Wilks	*F*-value	*P*-value
M. americana					
Population	25	198	0·142	47·947	<0·001
Maturation	25	198	0·568	6·021	<0·001
Population × maturation	25	198	0·743	2·745	<0·001
L. cyanellus					
Population	25	220	0·168	43·661	<0·001
Sex	25	220	0·643	4·889	<0·001
Population × sex	25	220	0·735	3·177	<0·001

d.f. (N), numerator d.f.; d.f. (D), denominator d.f.

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TABLE II. Cross-validation (%) of morphological characteristics for stunted juvenile (SJ), stunted adult (SA), non-stunted juvenile (NJ) and non-stunted adult (NA) *Morone americana*. Classification error was determined by jackknifed size-free, $\log_{10}$-transformed morphological characteristics

Morphotype	*n*	SJ	SA	NJ	NA	Error
SJ	31	77·4	22·6	0·0	0·0	22·6
SA	60	20·0	78·3	1·7	0·0	21·7
NJ	22	4·5	4·5	45·5	45·5	54·5
NA	113	0·0	0·9	25·7	73·5	26·5

n, the number of *M. americana* in the sample.

between morphotype and reproductive status was also significant (MANOVA, d.f. = 25, 198, $P < 0{\cdot}001$). The greatest degree of misclassification occurred between reproductive statuses within a morphotype (Table II). The greatest source of error was incorrect reclassification of non-stunted juvenile *M. americana* as non-stunted adult *M. americana*.

Shape differences

Shape deformation was greatest among stunted and non-stunted *M. americana* (Fig. 6). Among juvenile comparisons, grid deformation primarily was located in the mid-body portion of the stunted morphotype. Shape deformation among adult forms was similar to juvenile forms. Juvenile to adult shape deformation primarily was located within the postanal and head regions for stunted *M. americana*, whereas shape deformation was minimal for non-stunted *M. americana* with deformation located in the postanal region of the adult. The bending energy (*i.e.* the idealized energy required to deform the reference plot to the target plot) for the deformation was 0·015 between non-stunted juvenile and stunted juvenile *M. americana*, 0·019 between non-stunted adult and stunted adult *M. americana*, 0·011 between stunted juvenile and stunted adult *M. americana*, and 0·003 between non-stunted juvenile and non-stunted adult *M. americana*.

LEPOMIS CYANELLUS

Growth comparisons

Bivariate plots of canonical loadings of morphological distances from the DFA revealed distinct differences in morphology between stunted and non-stunted *L. cyanellus*. Based on visual inspection of the DFA plot, separation between the stunted and non-stunted morphotypes occurred along the first discriminant axis (Fig. 4), which explained 76·1% of the variation in morphological distances. Discrimination on this axis was primarily attributable to six measurements (Fig. 5), mostly concentrated in the head region. The morphological separation among stunted and non-stunted *L. cyanellus* was predominantly attributable to features in the head (Fig. 5).

There were significant differences (MANOVA, d.f. = 25, 220, $P < 0{\cdot}001$) between stunted and non-stunted *L. cyanellus* (Table I). Stunted female *L. cyanellus* and non-stunted male *L. cyanellus* demonstrated the greatest morphological separation.

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TABLE III. Cross-validation of morphological characteristics for stunted male (SM), stunted female (SF), non-stunted male (NM) and non-stunted female (NF) *Lepomis cyanellus*. Classification error was determined by jackknifed size-free ln-transformed discriminant analysis of morphological characteristics

Morphotype	*n*	SM	SF	NM	NF	Error
SM	59	55·9	35·6	1·7	6·8	44·1
SF	58	37·9	53·4	0	8·6	46·6
NM	83	6·0	1·2	79·5	13·2	20·5
NF	48	4·2	8·3	20·8	66·7	33·3

n, the number of *L. cyanellus* in the sample.

Few ($n < 10$) fish were incorrectly reclassified as stunted when non-stunted, and *vice versa* (Table III). The reclassification emphasized the morphological discrimination between stunted and non-stunted individuals.

Sex comparisons

Bivariate plots of canonical loadings of morphological distances from the DFA revealed differences between male and female morphology in the non-stunted *L. cyanellus*, whereas there was less difference between male and female morphology in the stunted *L. cyanellus*. The separation of male and female *L. cyanellus* morphology (based on inspection of the DFA plot) was along the second discriminant axis (DF 2), which explained 18·7% of the variation (Fig. 4). The separation of male and female *L. cyanellus* was predominantly attributable to five characteristics: distances from the origin of the pelvic-fin base to the origin of the anal-fin base, origin of pectoral-fin base to origin of anal-fin base and end of pectoral-fin base to origin of anal-fin base were greater in females, whereas the distance from the centre of eye to the pectoral-fin base was greater in males (Fig. 5).

There were significant differences (MANOVA, d.f. = 25, 220, $P < 0{\cdot}001$) between male and female *L. cyanellus*. The associated interaction between morphotype and sex was also significant (MANOVA, d.f. = 25, 220, $P < 0{\cdot}001$). The greatest degree of misclassification occurred between sexes within a morphotype (Table III). The greatest source of error was incorrect reclassification of stunted male *L. cyanellus* as stunted female *L. cyanellus*, and stunted female *L. cyanellus* as stunted male *L. cyanellus*.

Shape differences

Shape deformation was the greatest in comparisons of stunted and non-stunted *L. cyanellus* (Fig. 6). Shape deformation was primarily located in the mouth region and in the depth of the body. Shape deformation among female forms was similar with the male deformation, but not as great. Stunted-female to stunted-male deformation grid indicated very little change in form between the two sexes. Among the non-stunted *L. cyanellus*, deformation was primarily located in the mouth region and the preanal region. The bending energies for the deformations was 0·013 between non-stunted male and stunted male, 0·090 between non-stunted female and stunted female, 0·001 between stunted male and stunted female and 0·004 between non-stunted male and non-stunted female *L. cyanellus*.

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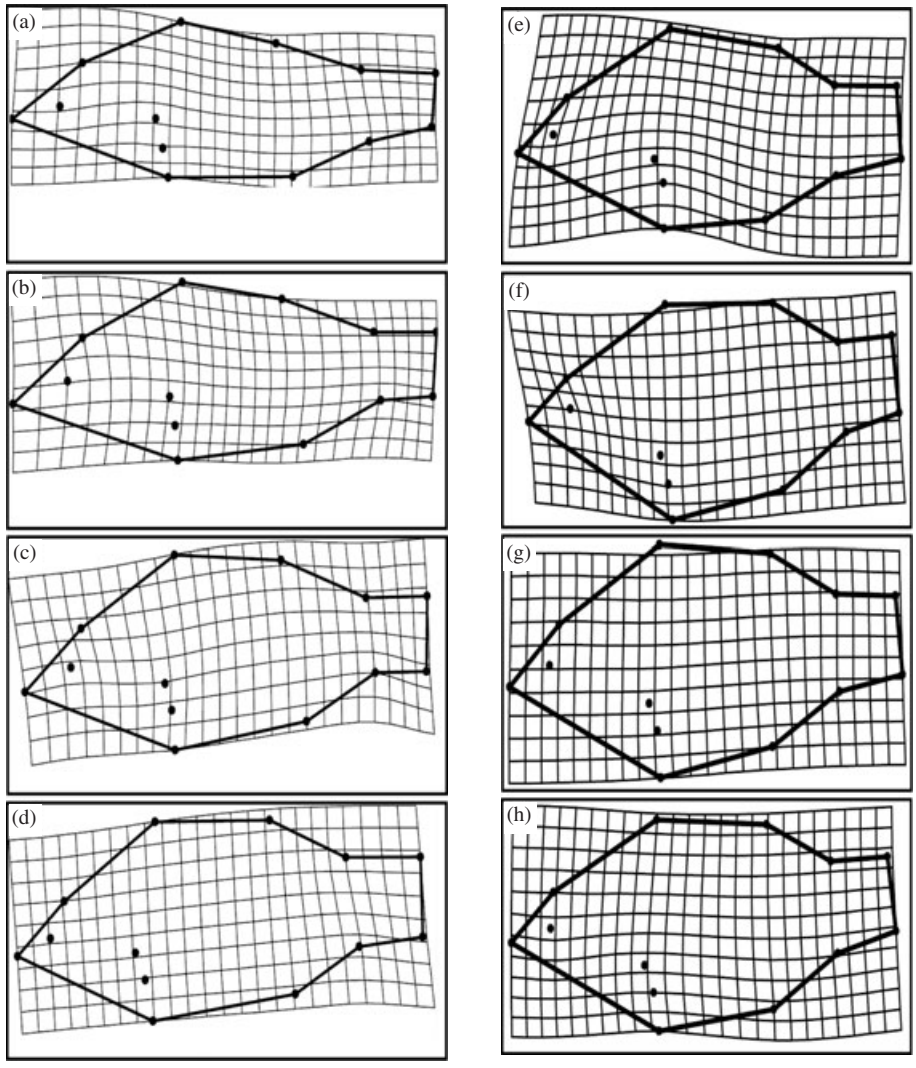

FIG. 6. Deformation grids depicting shape differences between (a) non-stunted juvenile and stunted juvenile, (b) non-stunted adult and stunted adult, (c) stunted juvenile and stunted adult and (d) non-stunted juvenile and non-stunted adult *Morone americana*. Deformation grids depicting shape differences between (e) non-stunted male and stunted male, (f) non-stunted female and stunted female, (g) stunted male and stunted female and (h) non-stunted male and non-stunted female *Lepomis cyanellus*. Shape deformation was magnified by $\times 2$ to allow for better visualization of the deformation. Landmark locations were standardized as shown in Fig. 3. If two morphotypes are identical, the output grid will contain straight lines where intersections of all elements are 90° angles.

DISCUSSION

Morone americana from Branched Oak and Pawnee reservoirs clearly differed in morphology. Likewise, *L. cyanellus* from the Justiceburg Pond and Mahon Pond clearly differed in morphology. Despite this consistency, features attributable to

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non-stunted fishes were inconsistent between the two species. Non-stunted *M. americana* displayed a much greater depth and length compared to the stunted *M. americana*, consistent with predictions and previous research. First, these results suggest that the *M. americana* were under sufficient size-dependent predation from local predators including *P. olivaris*, *M. salmoides*, *S. canadensis*, *S. vitreus* and *M. chrysops*. A deeper body acts to deter predation because predators typically select smaller, more fusiform prey (Wahl & Stein, 1988) and increases the probability of escape from attack by redirecting predator strikes away from the centre of mass (Webb, 1986). Second, these results provide an indication of the food resources available to the *M. americana* because deeper body forms are energetically costly (Chivers *et al*., 2008) due to increased hydrodynamic drag (Pettersson & Brönmark, 1997, 1999). Therefore, morphology of the non-stunted *M. americana* is consistent with previous studies, which suggest that predation and sufficient food resources prevent the population from becoming stunted in Pawnee Lake.

The deeper and longer body-form features observed in *M. americana* were not observed in *L. cyanellus*. The primary morphological feature attributable to non-stunted *L. cyanellus* was a greater snout length, a morphological adaptation to piscivory (Norton, 1995). There are two potential factors that may account for the disagreement with *a priori* predictions. *Lepomis cyanellus* were the only potential fish predators within Justiceburg Pond. Thus, predation may not have been sufficient to select for the deeper body form observed in other sunfishes in response to gape-limited predators (Januszkiewicz & Robinson, 2007). Second, food limitation may have influenced body form in the non-stunted *L. cyanellus*. Experiments by Chivers *et al*. (2008) showed that food limitation affected the amplitude of the response of morphology to predation. Given that the primary mode of predation in the Justiceburg Pond was cannibalism, there may not have been sufficient food resources available for the development of a deeper body form that could be distinguished from stunted *L. cyanellus*. In water bodies having greater availability of food resources and predation pressure, *L. cyanellus* may display the deeper body form. Further study is necessary to assess the role of different types of predators and food resources on the morphology of *L. cyanellus*.

Although there were morphological inconsistencies between the non-stunted *M. americana* and *L. cyanellus*, there were morphological consistencies among the stunted individuals. The stunted fishes from both populations had a larger head relative to the rest of their body. A large head in comparison to the rest of the body also has been observed in resource limited perch *Perca fluviatilis* L. (Olsson *et al*., 2007). Under food limitation, most energy is allocated to maintenance and little remains for somatic growth (Post & Parkinson, 2001). Under such conditions, bony structures grow continuously while the rest of the body remains undifferentiated, resulting in the development of fishes with large heads (Olsson *et al*., 2007). Like the morphology of non-stunted fishes, the morphology of the stunted fishes also is consistent with the suggested mechanisms (*i.e.* lack of sufficient predation, food limitation and dense populations) that may cause a population to become stunted (Roff, 1992; Ylikarjula *et al*., 1999).

Morphological differences between juvenile and adult forms of *M. americana* were greater in the stunted morphotype than the non-stunted morphotype. This finding was contrary to the *a priori* prediction that morphological divergence between juvenile and adult forms would be greater for faster-growing (non-stunted) fish than

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for slower-growing (stunted) fish. The juvenile period was approximately the same for stunted (Branched Oak Lake) and non-stunted (Pawnee Lake) *M. americana*, whereas longevity was much greater in stunted *M. americana* than in non-stunted *M. americana* (Chizinski, 2007). The difference in morphology between the juvenile and adult *M. americana* is probably related to plastic allometry (Schlichting & Pigliucci, 1998). Under normal growing conditions, energy is available for allocation to somatic growth, which has the effect of increasing the somatic tissue at a similar rate to the continuous growth of the bony structures. Thus, allometry of non-stunted *M. americana* would be relatively isometric, making shape differences less apparent between the juvenile and adult morphologies. Alternatively, stunted fish may allocate less energy to somatic growth because of food limitation, resulting in a body that remains undifferentiated compared to the bony structures in the head, as discussed previously. As stunted fish age, this difference becomes more pronounced, creating a greater morphological divergence between adult and juvenile fish.

The difference in morphology between the male and female forms of *L. cyanellus* was greater in the non-stunted morphotype than the stunted morphotype. This finding was consistent with the *a priori* prediction that morphological divergence between adult male and female forms would be greater for faster-growing (non-stunted) fish than for slower-growing (stunted) fish. In general, female *L. cyanellus* had a relatively deeper preanal area than male *L. cyanellus*, whereas male *L. cyanellus* had a relatively longer head region. The deeper preanal region in female *L. cyanellus* is biologically meaningful given the clear relationship of female body size and fecundity in fishes (Roff, 1983, 1984, 1992): females with a larger body cavity can produce a greater number of eggs. The DFA, however, indicates that these morphological differences between male and female *L. cyanellus* were less distinct in the stunted morphotype, despite female *L. cyanellus* having similar mass-adjusted fecundities (Chizinski, 2007). This difference in morphology suggests that food limitation, perhaps made more intense by *L. cyanellus* social behaviour (Hunter, 1963; Gross, 1980; Aday *et al*., 2006; Cooke *et al*., 2006), may be reducing the degree of sexual dimorphism in *L. cyanellus*.

The small size of the male and absence of sexual dimorphism observed in the *L. cyanellus* may have potential consequences for *L. cyanellus* social and reproductive biology. *Lepomis cyanellus*, like other centrarchids, exhibit parental care, which is an energetically expensive behaviour (Cooke *et al*., 2002, 2006). *Lepomis cyanellus* are colonial nesters, and males build and defend nests in the littoral zone where female *L. cyanellus* lay eggs throughout a protracted breeding season (Hunter, 1963). Nesting success of parental males primarily is determined by size and physiological condition (Calow, 1979; Webb, 2002) and decreased size or poor condition of the males may result in lower male reproductive success. Chizinski (2007) observed that stunted *L. cyanellus* were in poorer condition than non-stunted *L. cyanellus*, which suggests that stunted *L. cyanellus* may not have the energetic resources necessary to adequately defend their nests. Aday *et al*. (2002) observed that parental male *L. macrochirus* in stunted populations had lower nesting success than male *L. macrochirus* in non-stunted populations.

Typically, female *L. cyanellus* select larger males that are perceived to be better nest defenders (Hunter, 1963) but the absence of sexual dimorphism in stunted populations may have implications for mate choice, particularly the long-term consequences of reduced male size. For example, female *L. cyanellus* may preferentially

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select nesting males that have behaviours (*e.g.* greater aggressiveness) that allow them to better defend nests against predation. Changes in female mate choice might be observable by comparing recently stunted populations and historically, stunted populations. Female *L. cyanellus* may preferentially cue on alternative male morphologies as occurs in other species of sunfish. For example, female longear sunfish *Lepomis megalotis* (Rafinesque) have been shown to preferentially select males with longer opercular flaps (Goddard & Mathis, 2000). Stunted populations tend to remain stunted until a disturbance reduces the population biomass (*e.g.* addition of predators and winterkill); thus patterns of female mate choice may become evident through comparison of recently stunted populations and historically stunted populations.

As part of an assessment of cichlid *Amphilophus* spp. morphology, Parsons *et al.* (2003) compared traditional truss-based morphometrics with geometric methods and found that both methods are subject to the challenge of isolating shape variation from size variation. In this study of *L. cyanellus* and *M. americana*, both methods were also used and produced qualitatively similar results. Nevertheless, the traditional method is arguably more meaningful for studying the morphological differences between stunted and non-stunted fishes. These morphological differences probably first develop at small size, perhaps in the larval stage, and propagate throughout the life of the fish and, thus, are confounded with changes in size and allometry. Geometric methods that use thin plate splines to adjust for size differences do so isometrically by adjusting for the centroid size. Isometric scaling is ineffective when it is necessary to account for relative size differences, such as occur between stunted and non-stunted fish of the same species. Alternatively, the traditional method, which uses visual depiction of loading values does adjust for size differences allometrically and provides results that are easily interpretable and biologically relevant.

Although theoretical investigations into the proximate causes of stunting (Ylikarjula *et al.*, 1999) and empirical comparisons of life-history traits between stunted and non-stunted populations have been completed (Chizinski, 2007), morphological implications of stunted populations remain relatively unexplored. Examination of differences among stunted and non-stunted fish morphology provided insight into the interaction of predation and food limitation, two important mechanisms that influence stunted populations. In future studies, a combination of morphometrics and life-history analyses should be continued because of the complimentary information provided by both.

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